CHAPTER 3

PATTERNS OF TEMPERATE MARINE SPECIES DIVERSITY AT THE CONTINENTAL SCALE

Tim O'Hara

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3.1 Introduction

Recent evidence shows that local diversity can be influenced by regional diversity - the available gene pool in a given region (Ricklefs 1987). This chapter uses statistical approaches to describe and analyse large-scale patterns of diversity along the southern Australian coastline. This approach has been facilitated by the large number of marine surveys conducted in recent years, the recent preparation of comprehensive species lists (Rowe and Gates 1995; Dr. G.C.B. Poore in prep.), and the gradual addition of museum collection records onto computer databases.

This study represents the first attempt at a statistical analysis of southern Australian marine distributions. It avoids problems common in previous qualitative studies of:

- underestimating the tropical influence on the eastern and western coasts; and
- using separate definitions for the southern Australian region and the region occupied by the southern Australian fauna.

Regional diversity can vary along a continuous stretch of coastline according to large-scale environmental gradients and historical processes. Many researchers have observed a latitudinal (north-south) decline in faunal diversity from the equator to the poles. In a recent paper, Roy *et al* (1998) tested the change in diversity of marine prosobranch molluscs along the east and west coasts of North and central America against the median length of species ranges, the available area of continental shelves, sea-surface temperature and recent geological histories. Roy *et al* (1998) found that only sea-surface temperature explained observed trends, with peaks in diversity in warm water latitudes. However, other workers have demonstrated that not all taxonomic groups show peaks of marine diversity in warmer waters, for example macroalgae (Bolton 1994) and various groups of crustaceans (Brandt 1988; Barnard 1991; Poore and Lew Ton 1993).

Longitudinal gradients are poorly studied compared with latitudinal gradients (O'Hara pers. obs.). Southern Australia has one of the few extensive east-west coastlines (approx. 5,500 km) on the globe and permits the study of a large-scale marine longitudinal gradients in a temperate region.

Southern Australia (Figure 3.1) lies in the temperate zone with sea-surface temperatures ranging from 15.5 - 25°C in summer and 11.5 - 20°C in winter (Figure 3.2). The western and southern coasts lack major rivers and consequently carbonate sediments cover most of the continental shelves. The coast east of Wilsons Promontory in Victoria, in contrast, is dominated by siliceous sediments (see Ferns 1999). Tides are generally small, between 1 and 2.5 m, and much of the south and west coast is fully exposed to storm waves from the Southern Ocean (Bunt 1987).

The Leeuwin Current arises in warm Indonesian waters and in winter it flows south along the coast of Western Australia and then west into the Great Australian Bight. From here it is replaced by the warm saline Great Australian Bight Current (Rochford 1986) and then by the weaker Zeehan Current that runs as far east as the western coast of Tasmania (Baines *et al* 1983). The East Australian Current flows from the northern Tasman Sea south along the coasts of Queensland and New South Wales before veering off near 33°S back into the Tasman Sea. A series of warm-water eddies can be pushed further south into eastern Bass Strait and sometimes as far as the eastern coast of Tasmania (Cesswell 1987).

The shallow-water marine biota of southern Australia is generally described as being highly endemic, with estimates for various taxonomic groups ranging from 85 to 95% (Womersley 1981, Wilson and Allen 1987). The history of the fauna is complex (Poore 1994). The southern Australian coastline began forming in the late Cretaceous (90 million years ago) as western Australia started rifting away from Antarctica. The resulting marine intrusion was colonised by warm water species from the west. The east coast of Australia supported a cool water fauna that extended around Antarctica to what is now South America. Australia and Antarctica finally split around (40 to 35 million years ago) south of Tasmania, allowing the western and eastern faunas to mix. Since that time the evolution of endemic species in southern Australia has been enhanced by further invasions of tropical species as Australia drifted northwards towards south-east Asia and a smaller number of Southern Ocean species arriving by the circumpolar subantarctic currents.

The Pleistocene period has been marked by over 60 glacial-interglacial cycles (Teidemann *et al* 1994). Glacial periods in the region were characterised by lowered sea-levels (to 110 m below current sea-level) and cooler temperatures (Wells and Okada 1996). Bass and Torres Straits were generally dry (Chappell 1983; Blom 1988), the Subtropical Convergence (STC) moved north towards the southern Australian coastline (Wells and Okada 1996), and the Leeuwin Current ceased to flow around south-western Australia (McGowan *et al* 1997). The East Australian Current may have flowed further south however, no longer deflected by cool water flowing out of Bass Strait (Nees 1997). Several interglacials have experienced warmer conditions than at present (Howard and Prell 1992). During the last interglacial (125 thousand years ago) zooxanthellate corals were found as far south as Newcastle in New South Wales (Marshall and Thom 1976) and to 119°E in SW Western Australia (Kendrick *et al.* 1991) indicating a water temperature 1 - 2°C warmer than present. Several warm-temperate molluscs, foraminiferans and ostracods occurred in western Victoria (Collins 1953; Valentine 1965; Gill 1988; McKenzie *et al* 1990). For almost a century taxonomists have speculated that the emergence of Bass Strait during glacial periods would have promoted allopatric speciation by dividing a previously continuous fauna into two separate populations (Dartnall 1974).

Early studies into the distributions of southern Australian marine fauna and flora focused on delineating distinct regions or biogeographical provinces (eg Whitely 1932; Clark 1946; Womersley 1981). The details of these schemes differed but typically included:

- a Flindersian Province that extended from Bass Strait to Geraldton WA;
- a Peronian Province that extended from southern Queensland to Bass Strait; and
- a Maugean Province that included Bass Strait and Tasmania.

Wilson and Gillett (1971) simplified this scheme by recognising a broad temperate zone in southern Australia and a tropical zone in the north, with zones of overlap on the east and west coasts. More recently, researchers have focused on recognising groups of species that show coincident distribution patterns (eg Rowe and Vail 1982; Wilson and Allen 1987). Wilson and Allen's (1987) scheme includes a group of species with a general southern Australian distribution and other groups that are endemic to the west coast, the south-west coast, the south coast, south-east coast, and the east coast, with the regions of endemism overlapping considerably. Various distributional barriers have been identified for shallow-water species, including a sharp drop in temperature around Albany in WA, and the lack of shallow water reef habitat in the Great Australian Bight, Encounter Bay, and to the east of Wilsons

Promontory in Victoria (Hutchings quoted in Wilson and Allen 1987) for some reef-dependant marine species.

3.2 Methods

3.2.1 Study area

This study is restricted to shallow-water marine habitats (0 - 100 m) of Australia south of latitude 30°S. The deep-water fauna on the lower continental shelves and slopes was excluded, as these habitats experience different environmental conditions than the upper shelf and shore and may show a different pattern. Deep-water species were included only if they have been found on the upper shelf within the southern Australian region, excluding species that exhibit emergence in other climatic regions.

3.2.2 Taxa

The study includes all known species of decapods and echinoderms recorded from study area defined in 3.2.1 above (refer Table 3.1). It was intended to include molluscs in the analysis but imprecise locality data for many specimens and the difficulty of excluding published records based on dead shells made determining ranges for these animals problematic. Echinoderms and decapods are well known groups with a stable taxonomy and a long and extensive history of collection by scientists and naturalists. Both groups exhibit a range of life history and habitat patterns. Echinoderms typically have planktotrophic or lecithotrophic larvae (Giese *et al* 1991), although there are a number of brooding species in southern Australia (O'Loughlin 1991). Decapods typically have long-lived larvae (Sastry 1983) and inhabit a wider range of habitats than echinoderms including supratidal, estuarine and pelagic environments. Both groups also include large numbers of species that inhabit soft-sediment habitats.

Each species was placed into an *a priori* grouping based on shared distribution patterns (Table 3.2). These groups were intuitively derived and are used only to clarify geographical trends in species diversity. Species groupings based on clustering algorithms were unsatisfactory for this purpose (see results below).

3.2.3 Data acquisition

The shallow water marine environment across southern Australia was divided into a series of cells based on approximately one degree of latitude and longitude (Figure 3.1). Some neighbouring cells were merged to ensure that this study focused on variation along the coastline. Offshore cells that did not adjoin a coastline, or corner cells with a small amount of coastline, were merged with neighbouring cells. Cells within the major bays were merged with nearby open ocean cells (eg Spencer Gulf in South Australia). Bass Strait was divided up into two series of cells flanking the Victorian and Tasmanian coasts. The western side of Tasmania was excluded from the analysis as there has been very little collecting from that exposed and isolated coastline.

In total, the study area was divided into 57 cells. Each cell was numbered sequentially from Western Australia to Wilsons Promontory, across the north and east coast of Tasmania, and then from eastern Victoria to northern New South Wales.

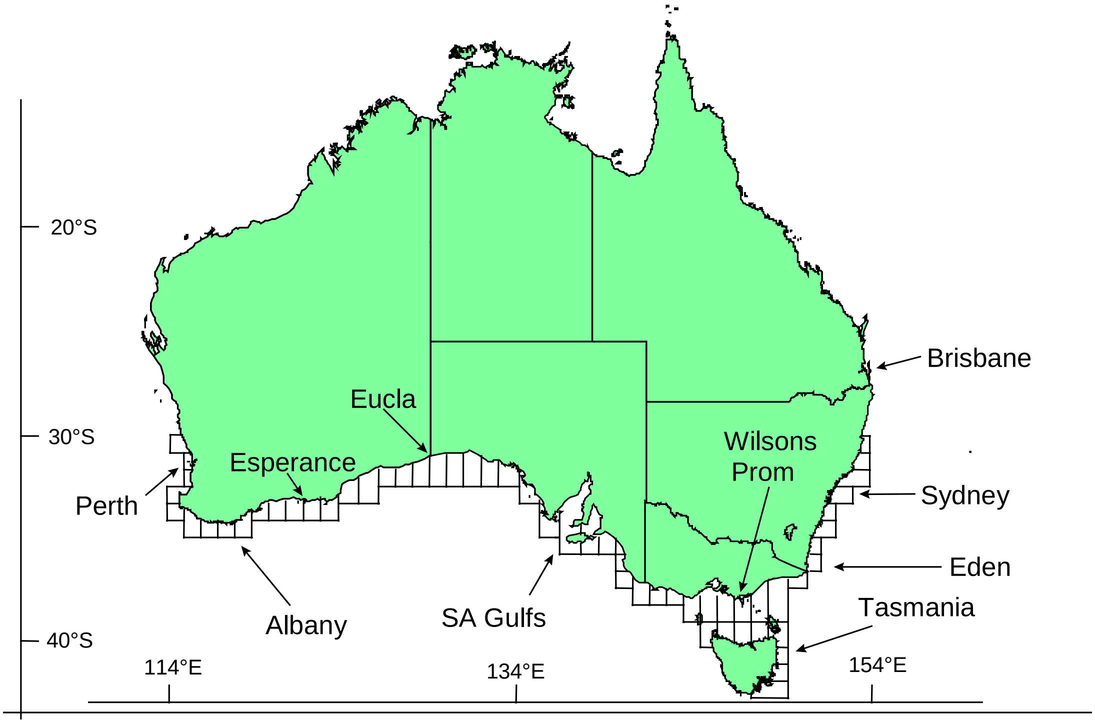


Figure 3.1 Map of Australia showing the location of the 57 cells used in this analysis.

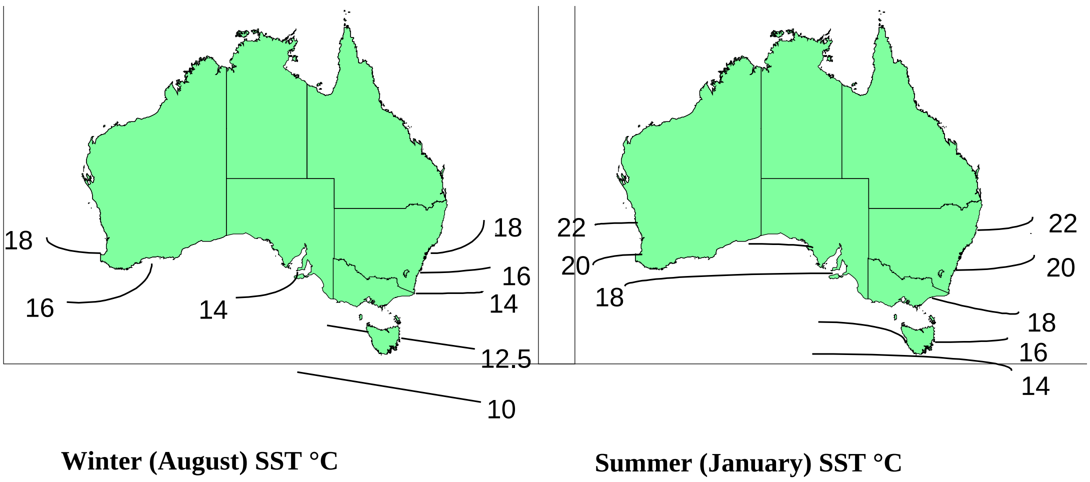


Figure 3.2 Maps of sea surface isotherms for August and January.

Taxonomic group	Common name	Number of species	Number of genera	Number of families
Echinodermata				
Crinoidea	Feather stars, sea lilies	32	19	11
Asteroidea	Sea stars	79	40	14
Ophiuroidea	brittle stars	89	41	13
Echinoidea	sea urchins	85	46	17
Holothuroidea	sea cucumbers	62	34	10
Subtotal		347	180	65
Decapoda				
Dendrobranchiata	prawns	90	6	2
Caridea	shrimps	15	35	10
Stenopodidea	coral shrimps	1	1	1
Thalassinidea	mud shrimps	25	15	7
Astacidea	lobsters, yabbies	-	-	-
Palinura	rock lobsters	12	7	2
Anomura	hermit crabs, porcelain crabs, squat lobsters	56	25	8
Brachyura	crabs	193	109	20
Subtotal		392	198	50
Total		739	378	115

Table 3.1 Decapod and echinoderm species recorded from shallow water (0 - 100 m) marine habitats from Australia south of 30°S.

Group	Description	Rule
Endemic	Restricted distribution	<= 5 cells
Flindersian -west	South-western species	< 138°E
Flindersian - east	South-eastern species	> 136°E to < 37°S
Flindersian	Western and southern species	< 136°E to < 37°S
Peronian	Eastern species	> 136°E to > 37°S
Southern	General southern species	< 136°E to > 37°S
Tropical	Indo-Pacific or cosmopolitan distribution	Occurs in the Indo-Pacific region
Temperate	All non-tropical species	

Table 3.2 *A priori* species groups based on shared distribution patterns. End points include: 138°E - western side of the South Australian Gulfs; 136°E - eastern side of the South Australian Gulfs; 37°S - south-central New South Wales.

The presence or absence of each species was recorded for each cell. Ideally distributional data would be derived from actual collection records. However, this requires even sampling along the coastline over an extended period of years, a task that is logistically unfeasible. Instead this study used species range data determined by identifying distributional limits from taxonomic publications and museum collections. Collections have been examined from the Museum of Victoria (Melbourne), Australian Museum (Sydney), South Australian Museum (Adelaide) and the Western Australian Museum (Perth). A species was scored as being present in a given cell, if the cell occurred within its known distributional range. A species range was assumed to be continuous across the coastline unless a distributional discontinuity was explicitly identified from the literature or from personal knowledge. Particular attention was applied to distributions in Bass Strait and around Tasmania. Isolated records from sites well outside the usual range of a species were excluded.

For the purpose of analysing species ranges and temperature limits, the grid system was extended to 24°S on either side of the continent. These additional cells contain range data only for species found in the original 57 cells and not additional tropical species.

Summer (January) and winter (August) sea-surface temperature data (SST) for each cell was derived from Comprehensive Ocean-Atmosphere Data Set (COADS) monthly temperature maps produced by the U.S. National Oceanic and Atmospheric Administration (NOAA).

3.2.4 Statistical methods

The presence-absence species-cell matrix was analysed using various graphical and multivariate statistical techniques available in the PATN and PRIMER software packages (Belbin 1993; Clarke and Warwick 1994). The Bray-Curtis association coefficient was used to measure similarity between cells in all cases. Classifications were derived using the PRIMER hierarchical agglomerative clustering technique. The Semi Strong Hybrid multi-dimensional scaling (SSH) and DEtrended CORrespondence ANAlysis (DECORANA) methods of ordination in PATN were used in order to reduce the artificial curving of data-points that can occur when dealing with datasets with strong linear gradients (Gauch 1982; Belbin 1993). Detrended correspondence analysis has the advantage that distance between points is expressed in units of species turnover, but the practical disadvantage that the PATN version of the algorithm is limited to 500 species, preventing an analysis of the entire dataset.

The ordination stress values for the two-dimensional ordinations were very low (0.06). Environmental data (latitude, longitude, summer and winter sea surface temperature) were correlated with the SSH ordination using the Principal Axis Correlation routine (PCC). PCC is a multiple-linear regression routine in PATN designed to see how well intrinsic or extrinsic variables can be fitted into ordination space (Belbin 1993). The correlation vectors were superimposed on the ordination plot, the length of each vector giving an indication of strength of the correlation. The PRIMER BIOENV procedure, using a weighted Spearman rank correlation, was also used to rank the group of environmental variables that best matched the species occurrence in each cell. Correlations and multiple regressions were performed using the STATISTICA software package.

3.3 Results

3.3.1 Patterns of species distributions

The change in species richness along the coastline is shown in Figure 3.3. The pattern was broadly similar for both taxonomic groups and the combined dataset is illustrated here. The overall levels of species richness are broadly similar across the entire coastline (median = 242) with peaks recorded around Perth (356), Sydney (366), the South Australian Gulfs (295), Port Phillip Bay (276) and Western Port (280), and a trough in south-eastern Tasmania (195). The peaks correspond with major population centres and thus possibly with collecting effort. However, examination of the species groups contributing to these peaks indicates that Perth and Sydney are areas of genuine overlap between tropical and southern faunas. There are large numbers of tropical species that have a southern distribution limit just near these cities and also a number of southern species that have a northern distribution limit at the same point. The western peak of diversity (31°S) is 2 degrees further south than the eastern peak (33°S). The peak in the South Australian Gulf region is due to the large number of local endemics (16) and overlapping south-eastern and south-western faunas. The peak in richness in the Victorian bays is due to a small number of local endemics (5) and an overlap between the south-coast fauna and eastern faunas. Although south-eastern Tasmania supports a number of local endemics (9), it is not enough to compensate for the drop-off in species along the northern and eastern coasts of Tasmania. Overall the trend is for a latitudinal gradient in species richness from the subtropics to Tasmania. There is an apparent decline in species richness to the north of Perth and Sydney caused by the rapid reduction of the southern fauna. However diversity can be expected to peak again further to the north as there are far more species of both echinoderms and decapods known from tropical than temperate Australia (Rowe and Gates 1995; G.C.B. Poore pers. comm.).

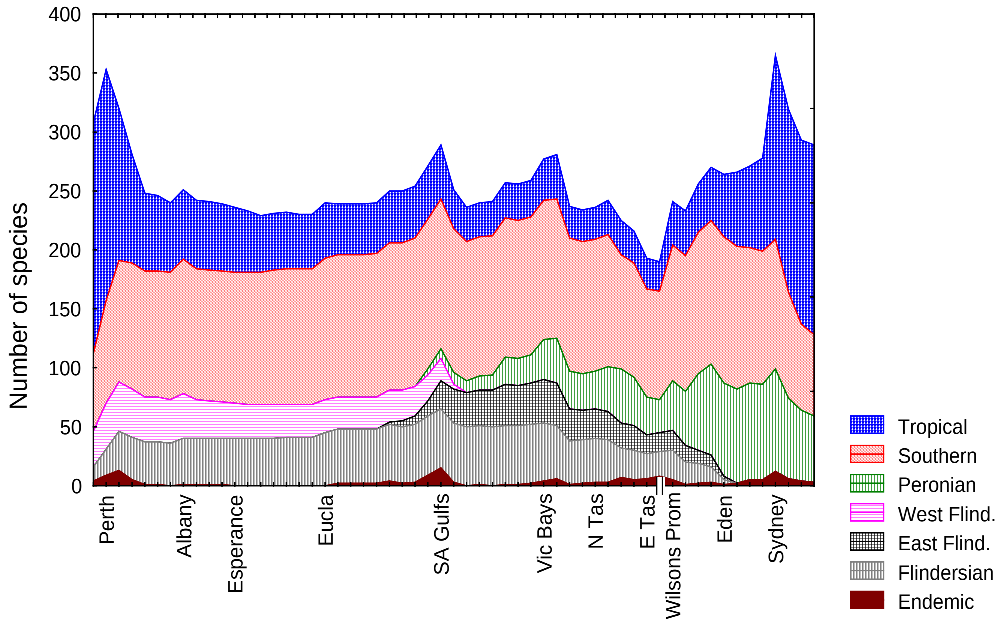


Figure 3.3 Stacked plot of species richness along the southern Australian coastline. Species groups are described in Table 2. Scale break on bottom axis indicates cell sequence discontinuity between southern Tasmania and eastern Victoria.

There is no indication of a correspondence of species richness with width of continental shelf. Shelves are relatively narrow at points of peak species richness around Sydney and Perth. Areas with wide continental shelves, for example, the Great Australian Bight or Bass Strait, support only average species richness.

Further collecting effort would lead to an increase in known species ranges. This may have the effect of smoothing out the peaks and troughs on the species-richness gradient. However, it is equally plausible that more species will be found in the regions of species overlap. It is also possible that more species will be found to have disjunct distributions, being restricted to patches of discontinuous habitat such as estuaries or seagrass beds. This also may accentuate species richness in the cells that include large embayments.

The turnover of species between cells is shown in Figure 3.4. The points of greatest species turnover are similar to the peaks and troughs on the species-richness curve. A large number of tropical and southern species have distributional end-points around Sydney and Perth, other regions of high species turnover include the South Australian Gulfs, central Victoria, southern New South Wales, and along the northern, eastern and south-eastern coasts of Tasmania. The overall east-west turnover of species is high with only 142 species occurring at both Sydney and Perth and 134 shared between Albany and Eden.

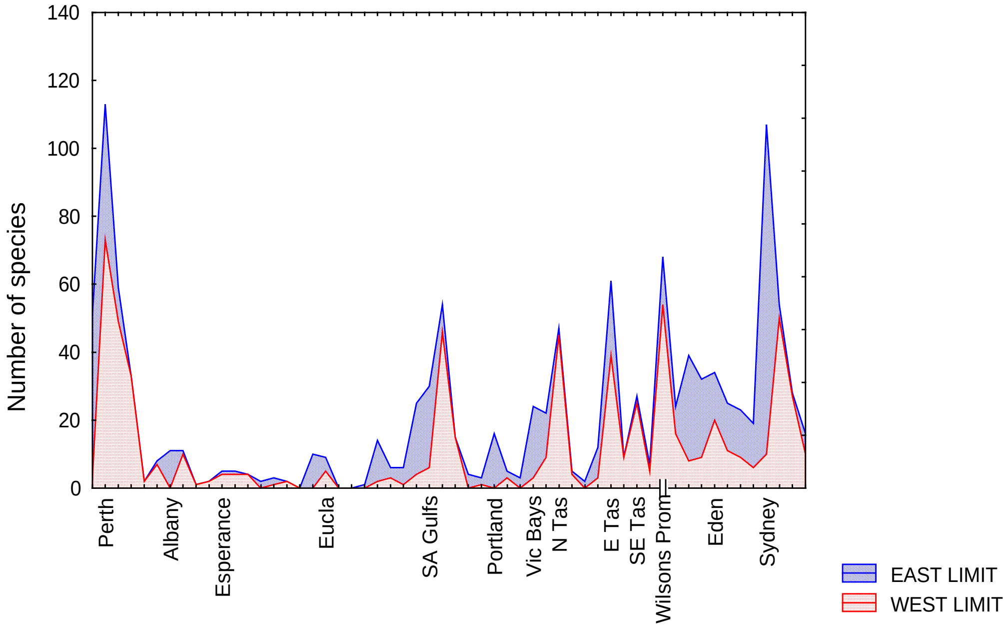


Figure 3.4 Stacked plot of species turnover along the southern Australian coastline.

The number of cells occupied by each species can be used as a surrogate for length of a species range. The graph showing the relationship between number of species and number of cells occupied by each species is shown in Figure 3.5. This graph is restricted to 435 species that do not extend further into tropical Australia than 24°S, and thus excludes some species with large distributional ranges. After an initial peak of narrow-ranged species there is a slight decline in the number of species with progressively larger ranges. Over 10% (76) species are currently known from five or fewer cells. For those species known from relatively few records, this may reflect low abundance as much as a narrow geographical range. Other species have well-established narrow ranges (eg the asteroids *Patiriella vivipara* from south-eastern Tasmania and *P. parvivipara* from Ceduna in South Australia). A graph showing the distribution of narrow-range species is given in Figure 3.6.

The average range size of species occurring at each cell is given in Figure 3.7. Again this graph is restricted to southern endemics occurring only below 24°S. The graph shows inverse patterns of species richness and average range size, although the two variables are not correlated (r = -0.03). Species richness of southern endemics tends to increase slightly from east to west, while average range size decreases. Local areas of species richness (eg the South Australian Gulfs and the Victorian bays) are marked by low points of average range size.

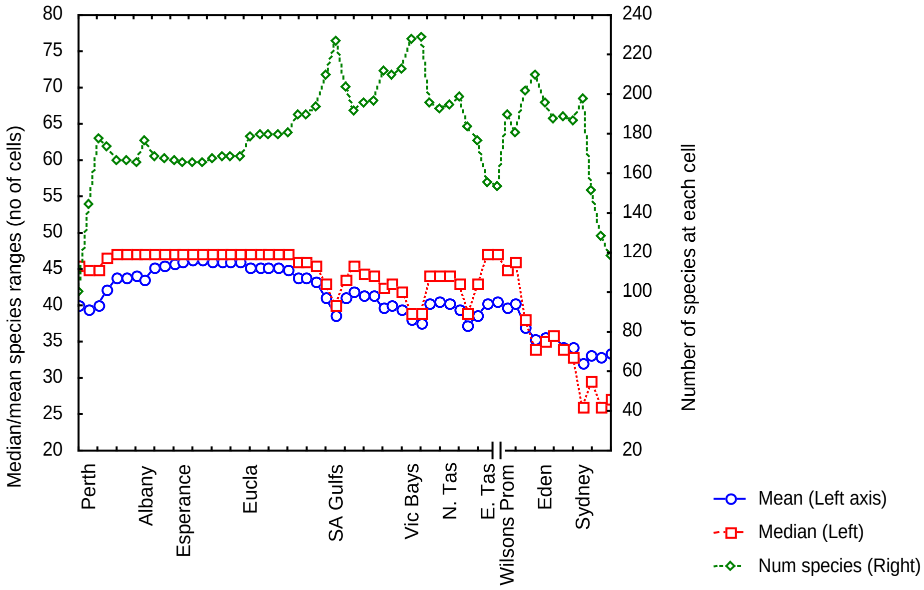


Figure 3.5 Line plot of average range size for the 435 echinoderm and decapod species restricted to Australia south of 24°S.

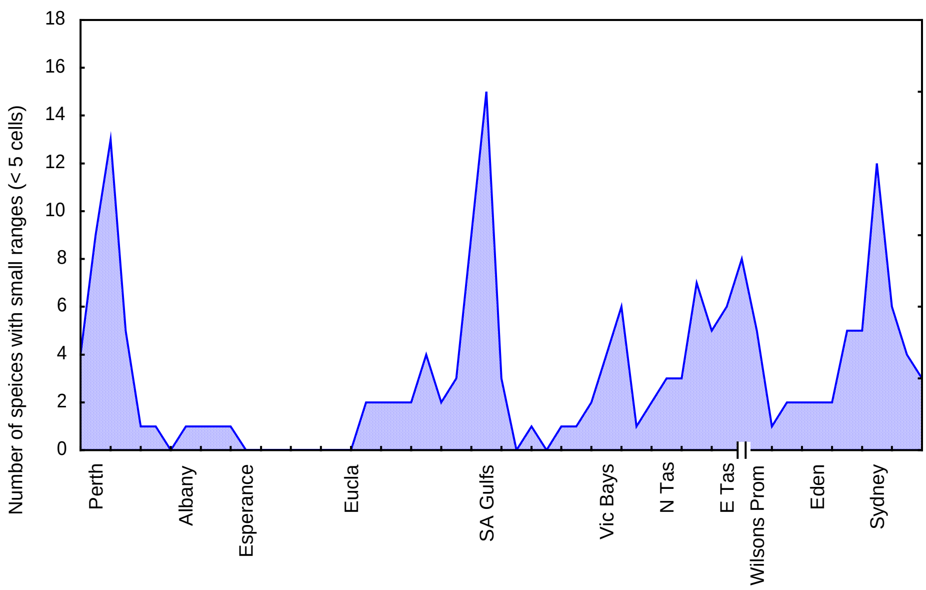


Figure 3.6 Distribution across southern Australia of species with small ranges (< 5 cells).

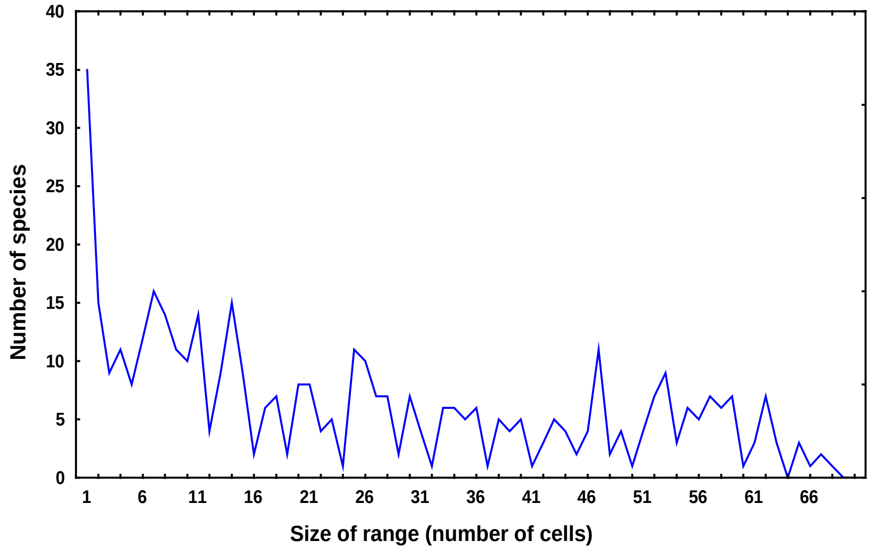


Figure 3.7 Line plot comparing number of species with increasing range size.

Computing the levels on endemism amongst echinoderms and decapods in southern Australia depends how the region and the endemic fauna are defined (Table 3.3). The 739 species in this dataset includes 296 Indo-Pacific species (40%), another 183 predominantly southern species (25%) that extend north of 30°S, and a further 14 species (2%) that occur elsewhere (eg New Zealand, Southern Ocean) (Table 3.4). Only 37% of species can be said to be strictly endemic to the region below 30°S. If the region is narrowed to the south coast only 21% are strictly endemic.

Only by using a broad definition of the Southern Australian fauna (including species that range into subtropical Australia) and a narrow definition of the region (Albany to Eden) can the figures be interpreted as approaching the high levels of endemism recorded by previous biogeographers (74%). This emphasises the overlapping nature of the tropical and temperate faunas.

Definition of region	Number of species	Definition of southern Australian endemic fauna	Number of endemic species	% endemism
Australia south of 30°S	739	Restricted to region south of 30°S.	256	37 %
		All "southern" species	411	56 %
Southern coast of Australia from Albany WA to Eden NSW	489	Restricted to the region between Albany and Eden	100	21 %
		All "southern" species	356	74 %

Table 3.3 Levels of endemism shown by echinoderms and decapods. 'Southern' species are defined as those that occur predominantly in southern Australia but may range into tropical Australia on either side of the continent.

Genus	Taxonomic group	Number of species occurring in southern Australian region	Number of southern Australian species (excluding Indo-Pacific species)
Alpheus	Caridea	24	9
Amphiura	Ophiuroidea	18	9
Synalpheus	Caridea	12	2
Nectria	Asteroidea	8	8
Paguristes	Anomura	8	8
Pilumnus	Brachyura	8	8
Ophiothrix	Ophiuroidea	8	5
Upogebia	Thalassinidea	7	4
Amblypneustes	Echinoidea	7	7
Portunus	Brachyura	7	1
Thalamita	Brachyura	6	0
Patiriella	Asteroidea	6	6
Athanas	Caridea	6	0
Ophiactis	Ophiuroidea	6	2
Charybdis	Brachyura	6	2
Holothuria	Holothuroidea	6	2
Plesiocolochirus	Holothuroidea	5	2
Palaemon	Caridea	5	4
Echinaster	Asteroidea	5	3
Galathea	Anomura	5	2
Ophiacantha	Ophiuroidea	5	4
Diogenes	Anomura	5	3
Cenolia	Crinoidea	5	5
Dardanus	Anomura	5	1
Astropecten	Asteroidea	5	2

Table 3.4 List of speciose genera occurring in southern Australia.

3.3.2 The distribution of species across Victoria

Just under half (49%) of the total species (739) occur in Victoria (362 species). The species richness of each grid across Victoria (and northern Bass Strait) is given in Table 3.5. The species richness is relatively constant across the State. The mean is 256 species, with a maximum at Western Port Bay (280) and a minimum (232) at Delray beach east of Wilsons Promontory.

The Victorian fauna can be divided into four categories:

- a ‘common’ group that occur throughout Victoria;
- a ‘western’ group that has a eastern limit in Victoria;
- an ‘eastern’ group that has a western distribution limit within Victoria; and
- a ‘central’ group that occurs in central Victoria but not at the eastern of western limits of the State (see Table 3.6).

The ‘central’ group is characterised by species endemic to Victoria only (including species that are limited to Victoria’s bays and inlets which mainly occur in central Victoria), and species that occur more widely, but within both Victoria and Tasmania waters. Approximately one half of all species (51%) in this group are distributed throughout the State, the other half (49%) have a distribution limit at some point within Victoria (in other words there is a almost 50% turnover of species across the State).

The distribution limits of species generally occurs between Port Phillip Bay and Wilsons Promontory / Nooramunga (Figure 3.4), although some 'western' species continue further east, and some 'eastern' species further west. A group of common New South Wales species (n = 61) extend to the far east of the State. Species restricted to western Victoria (west of Cape Otway) are limited to a few shelf species that are presumably limited by the shallow waters of Bass Strait (eg the anomuran *Strigopagurus elongatus*).

Grid no	**Latitude (ºS)**	**Longitude (ºE)**	**Location**	**Number of Species**
34	38	141	Portland	256
35	38	142	Warrnambool	255
36	39	143	Cape Otway	258
37	39	144	Port Phillip Bay	276
38	39	145	Western Port Bay	280
50	39	146	Wilsons Promontory	240
51	39	147	Ninety Mile Beach	232
52	39	148	Lakes Entrance	255
53	38	149	Far eastern Gippsland	269

Table 3.5 Species richness of echinoderms and decapods across Victoria.

Victorian distribution	**Grid presence**	**Crustacea**	**Echinodermata**	**Total**
All Victorian	Occurs through Victoria	104	80	184
Western	Occurs in the far western grid (34) but not the far eastern grid (52)	33	39	72
Eastern	Occurs in the far eastern grid (52) but not the far western grid (34)	46	39	85
Central species	Doesn't occur in the far eastern (52) or far western grid (34)	11	10	21
Total		194	168	362

Table 3.6 Distribution of Victorian species (grid numbers are given in Table 3.5 above).

3.3.3 Cluster diagrams

Cluster diagrams of the cells differed for echinoderms and decapods and are shown separately in Figures 3.8 and 3.9. The cluster algorithm orders the cells sequentially along the coastline, this is expected for grid analysis where cells are related to their neighbours through shared species distributions. Both cluster diagrams identify cells at the extreme north of the range (to Perth and Sydney) as being separate from more southerly cells. The primary division in decapods is located to the east of the South Australian Gulfs with a secondary division of the eastern cluster at Wilsons Promontory. For echinoderms the situation is reversed, the primary division is at Wilsons Promontory and the secondary division of the western cluster is at the eastern edge of the South Australian Gulfs. At the lowest level the clusters are composed of 3 - 5 neighbouring cells corresponding to geographically distinct sections of the coastline, for example northern Tasmania, east-southern Tasmania, eastern Victoria, southern New South Wales. The cluster diagram for the combined dataset reflects the more numerous decapod subset and is not shown. Cluster diagrams for species (not shown) were prepared but were unsatisfactory for the purpose of identifying groups of species with similar distributions as the algorithms could not distinguish between tropical species ranging into southern Australia and east-coast and west-coast endemics.

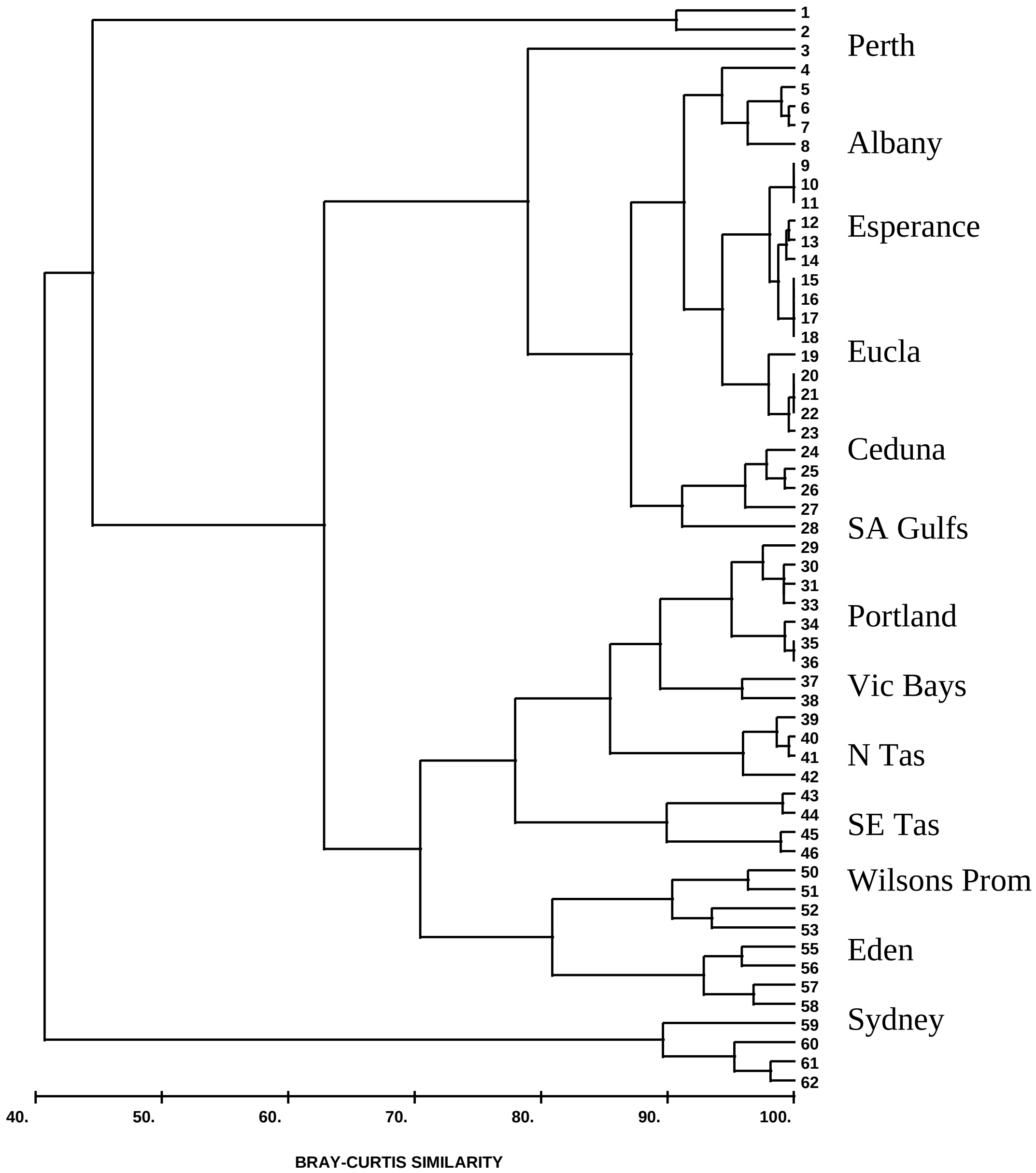


Figure 3.8 Cluster diagram of sites for decapod species.

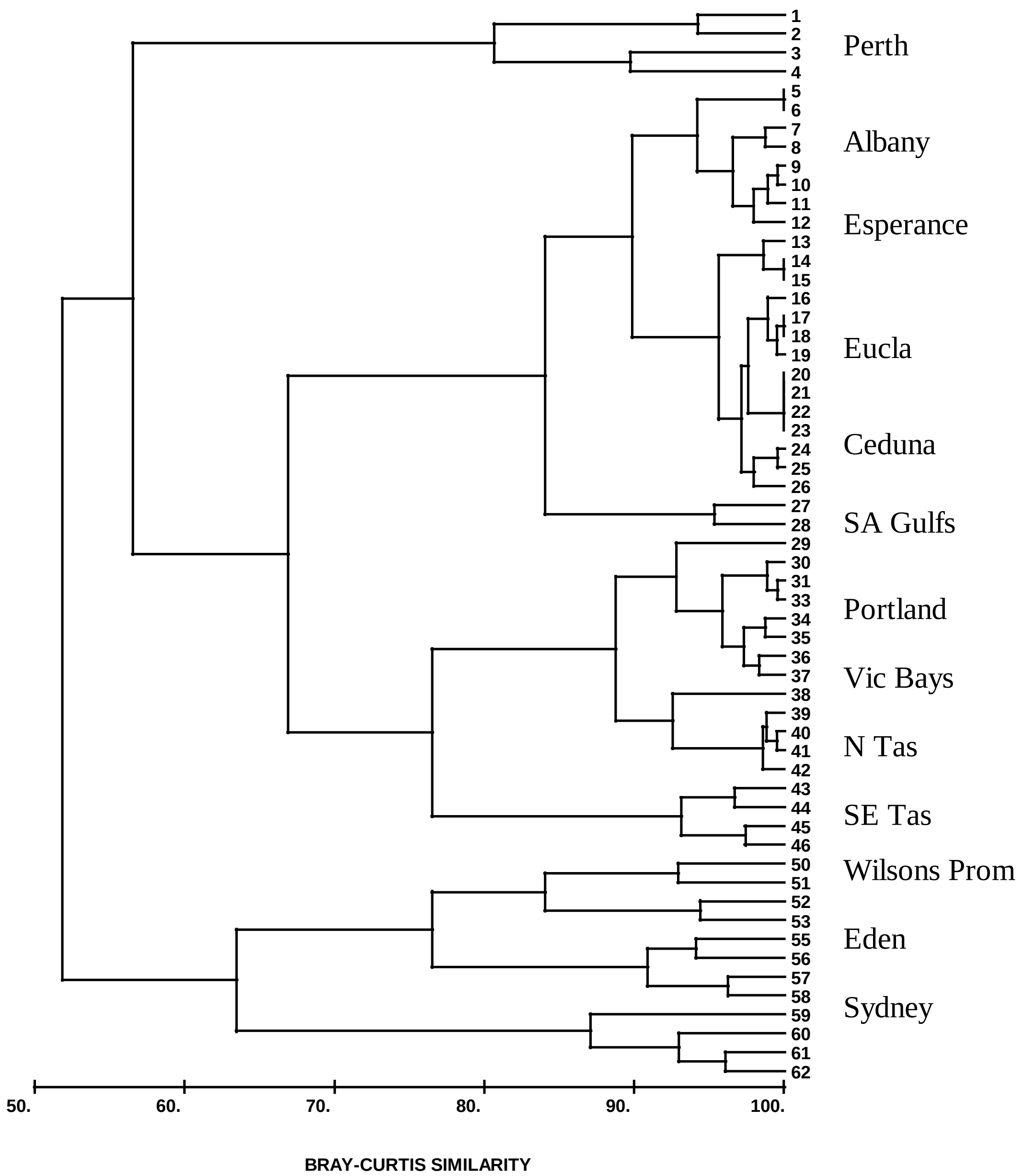


Figure 3.9 Cluster diagram of sites for echinoderm species.

3.3.4 Ordinations

The SSH ordination for the combined dataset is shown in Figure 3.10. Again the data points are laid out sequentially in a curve across the ordination plot. The shape is reminiscent of a map of Australia with the northern cells lying at the top ends of the curve, and the cells from eastern Tasmania placed separately at the lower right corner. The curve is not an artefact but an outcome of the shared distribution of tropical species between the most northerly cells.

The DECORANA ordination for the echinoderm dataset is shown in Figure 3.11. Most of the variation is along the bottom (longitudinal) axis. It shows a rapid turnover of species along the west coast and to a lesser extent along the coast of eastern Victoria and New South Wales. Major faunal breaks occur at the South Australian Gulfs and between western and eastern Bass Strait.

PCC multiple regression vectors have been superimposed on the SSH ordination plot (Figure 3.10). These vectors show that axis 1 is strongly correlated with longitude and axis 2 with temperature and inversely with latitude. The PCC correlation coefficients are slightly higher for longitude (0.9641), August sea surface temperature (0.9553) and January sea surface temperature (0.9384) than latitude (0.8844).

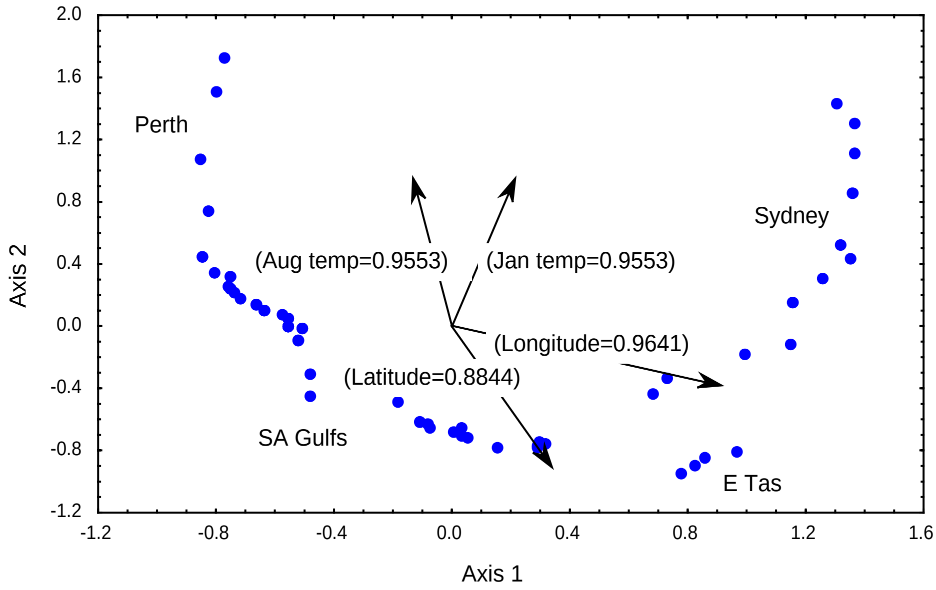


Figure 3.10 Biplot of SSH Ordination overlain with PCC vectors. The strength of the correlation is given in brackets next to each vector.

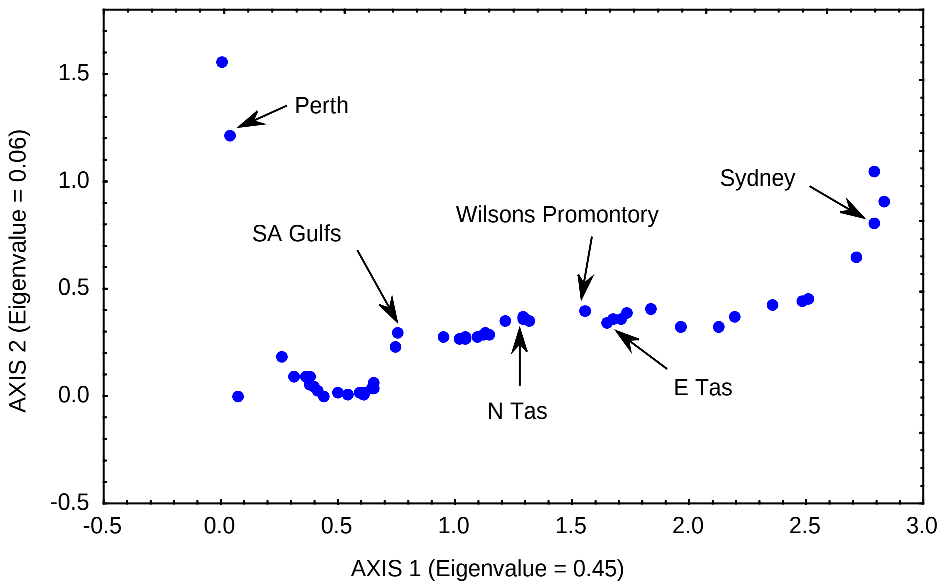
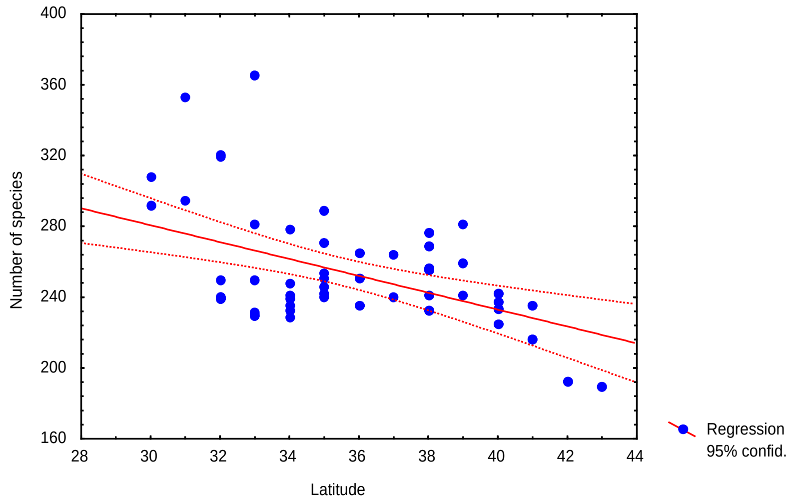


Figure 3.11 Detrended Correspondence Analysis ordination of 347 echinoderm species.

3.3.5 Temperature correlations

Species richness is correlated with January sea surface temperature (r = 0.70 at p < 0.05), August sea surface temperature (r = 0.61) and latitude (r = 0.45) but not with longitude. Scatter-plots of species richness against latitude and January sea surface temperature are shown in Figure 3.12. The outliers on both graphs represent the peaks and troughs of species richness discussed earlier. These linear correlations do not fully account for the drop in species richness north of Perth and Sydney, the peaks of diversity in central Victoria and the South Australian Gulfs, and the lack of species richness in the relatively warm northerly waters of the Great Australian Bight (32°S). The graphs exhibit similar scatter when species richness is log or double-square-root transformed. Sea surface temperature is more strongly correlated with species richness because it better accounts for the more southerly peak of species richness on the west coast (summer temperature of 21.6°C at 31°S compared to 23°C at 33°S on the east coast) and the peak of species richness in the SA Gulfs where a strong north-south temperature gradient can exist in summer months (Figure 3.13). Latitude and sea-surface temperature are highly correlated (Pearson's coefficient r = -0.73 for summer isotherms and r = -0.81 for winter isotherms at p <0.05) and cannot be used as separate independent variables in a multiple regression with species richness.



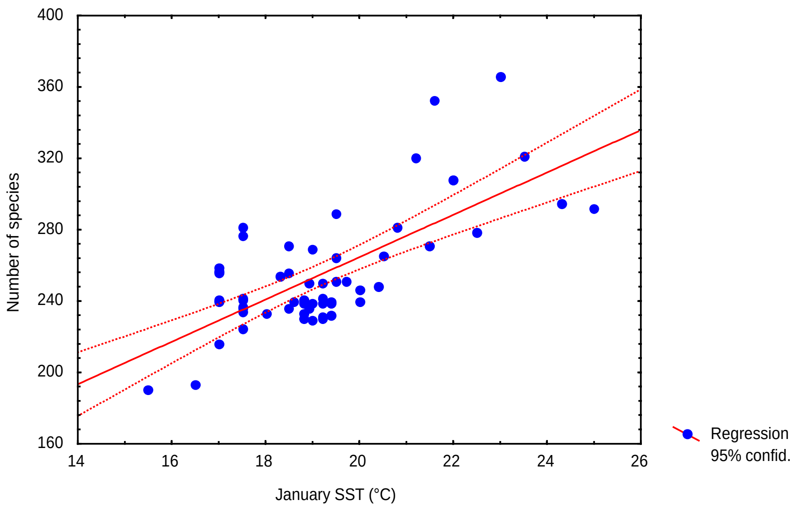


Figure 3.12 Scatterplots of species richness with latitude (R = -.4703) (top) and summer sea surface temperature (R = .70455) (below).

3.3.6 Temperature and species distribution limits

To further explore the effects of temperature on species distributions, the end-points of species ranges on the eastern and western coastlines were compared for symmetry. The hypothesis was that if temperature was the key factor that determined distributions, species ranges should finish at approximately the same isotherm on each coast. The expectation was that the temperature differential between east and west summer temperature would form a normal distribution around 0°C. Northern distribution limits (maximum summer temperature) and southern distributional limits (minimum summer temperature) were treated separately.

The maximum sea surface temperature analysis was restricted to species that extended northwards from either side of Bass Strait (a temperature minimum) and had distributional end-points within the scope of this analysis (below 24°S). A graph showing the number of species against maximum summer temperature difference is shown in Figure 3.14. Mean temperature difference was 2.03°C and standard deviation 3.42°C. There is no obvious relationship between eastern and western maximum temperature limits with the majority of species tolerating higher temperatures on the east than the west coasts. Some examples of range asymmetry include the Eastern Rock Lobster *Jasus verreauxi* (Port MacDonnell to southern Queensland), the callianassid shrimp *Biffarius arenosa* (Portland to Moreton Bay) and the ophiuroid *Ophiocentrus pilosa* (Spencer Gulf to Fraser Island).

The minimum temperature analysis was restricted to species that occurred on both the east and west coasts and had a distributional limit (a minimum temperature tolerance) somewhere on the southern coast. Species that range into Tasmania were excluded as the lack of data from the west coast precludes an east-west comparison. Species included tropical species that range to some extent down the east and west coasts and temperate species that have disjunct eastern and western populations.

A graph showing the number of species against minimum winter temperature difference is shown in Figure 3.15. Mean temperature difference was -0.54°C and standard deviation 2.74°C. The graph is bimodal. There is a group of tropical species that tolerate lower temperatures on the west coast compared to the east coast, and a group of tropical and temperate species with no temperature differences. This last group of species, apparently limited by a minimum winter isotherm, can be divided up into three groups.

- Species limited to the 20 - 16°C isotherms

  Most of these species are wide-ranging tropical forms (eg the ophiuroids *Ophiothela danae* and *Ophiocoma dentata)* that range into SW Western Australia and central New South Wales. However, two decapods have disjunct subtropical distributions: *Macrophthalmus punctulatus* (around Albany and Sydney to Brisbane) and *Pagurus sinuatus* (Shark Bay to Albany and Batemans Bay to Sydney). A number of subtropical species-pairs can also be recognised, for example, the ophiuroids *Ophiocoma occidentalis* (WA)/*O. endeani* (NSW-QLD) and *Macophiothrix michelseni* (WA)*/M. lampra* (NSW) (Devaney 1970, Hoggett 1991).

- Species limited to the 14.5 - 13.5°C isotherms

  This group also contains some tropical species (eg the decapods *Ephippias endeavouri* and *Synalpheus streptodactylus*) that range as far along the south-west coast as Victor Harbour, South Australia and along the south-east coast to Eden, New South Wales or into eastern Victoria. There are also a number of species with two disjunct populations. These include the ophiuroids *Clarkcoma pulchra*, *Ophiothrix spongicola* and

Ophiopsammus assimilis, the callianassid shrimp *Upogebia australiensis* and the brachyuran crab *Ozius truncatus.* Molluscan examples include the gastropod *Turbo torquatus* and the opisthobranch *Elysia coodgeensis* (R. Burn *pers. comm.*). The echinoids *Phyllacanthus parvispinus* (Queensland to Gabo Island, Victoria)/*P. irregularis* (Perth to the South Australian Gulfs) are a possible species-pair (Rowe and Hoggett 1986).

- Species limited to the 13°C isotherm

  A few animals range into northern Bass Strait but are absent from the northern Tasmanian coastline. Examples include the ophiuroid *Ophiocrossota multispina* and the tropical carid shrimp *Alpheus sulcatus*.

Species with a lower minimum temperature cannot be recognised with this analysis because of the lack of comprehensive data collection on the western coastline of Tasmania. However, where records are available there appears to be a group of species limited to the 12.5°C winter isotherm, which intercepts the eastern and western extremities of the northern coast of Tasmania (eg the echinoderms *Plectaster decanus*, *Lipotrapeza vestiens*, *Taeniogyrus roebucki*) (Edgar *et al* 1997; T. O'Hara unpublished data).

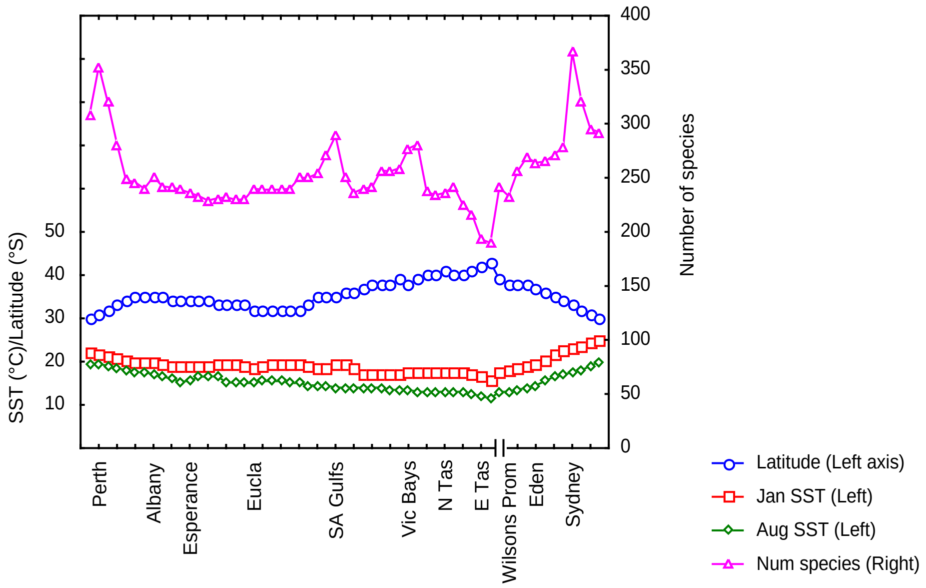


Figure 3.13 Line plot comparing trends of species richness, latitude and sea surface temperature (SST).

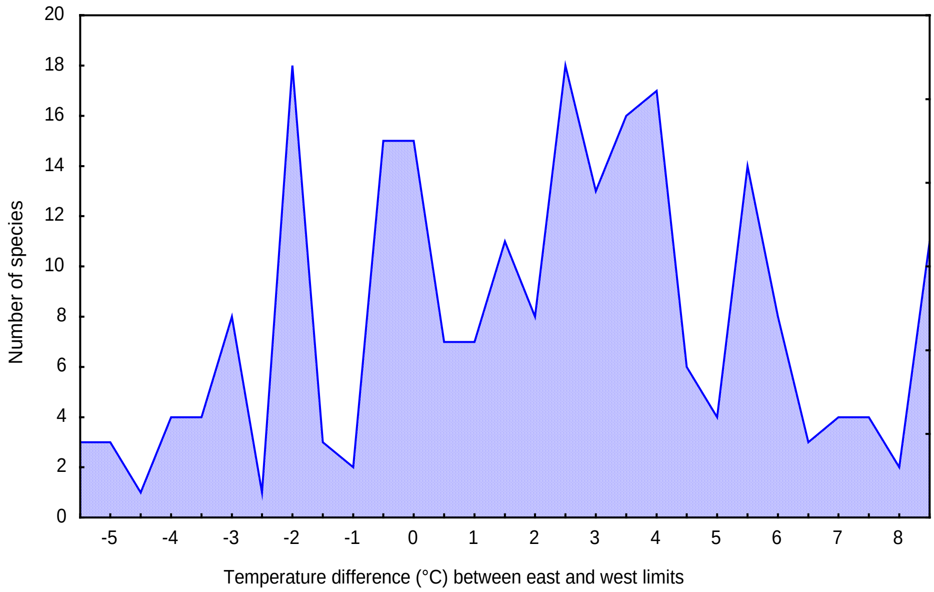


Figure 3.14 Differences in summer sea surface temperature between northern distribution limits on the east and west coasts.

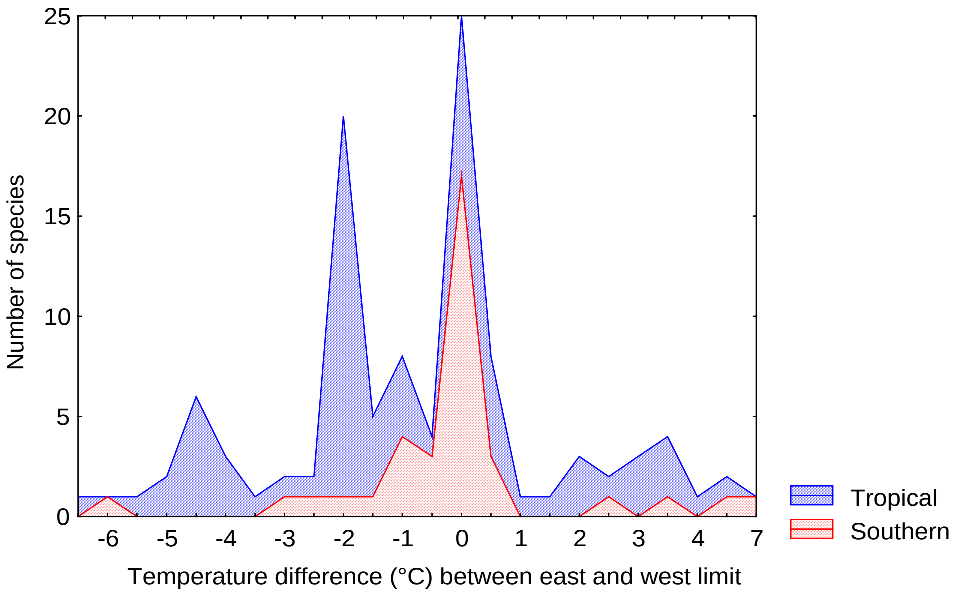


Figure 3.15 Differences in winter sea surface temperature between southern distribution limits on the east and west coasts.

3.3.7 Taxonomic diversity

The mean number of species per genus is 1.96 (std dev = 2.05) and species per family is 6.43 (std dev = 8.01). The relationship between genera and numbers of species is shown in Figure 3.16. The majority of genera (79%) have only one or two species occurring in southern Australia. If one considers only those species endemic to below 30°S then 88% of genera only have 1 - 2 species. Genera with 5 or more species are listed in Table 3.4. The majority of these genera are widespread with numerous species scattered in different regions of the world. None of these speciose genera are endemic to southern Australia with the possible exception of the asteroid genus *Nectria*, which has a dubious New Zealand record (Rowe and Gates 1995). Several other genera are restricted to the Tasman region including

Amblypneustes and *Cenolia*. The asteroid genus *Patiriella* is known to be polyphyletic and should not be considered as a single genus (Hart *et al* 1997). In summary, evolutionary radiation of echinoderms and decapods in Southern Australia has been limited to a small number of widespread species-rich genera.

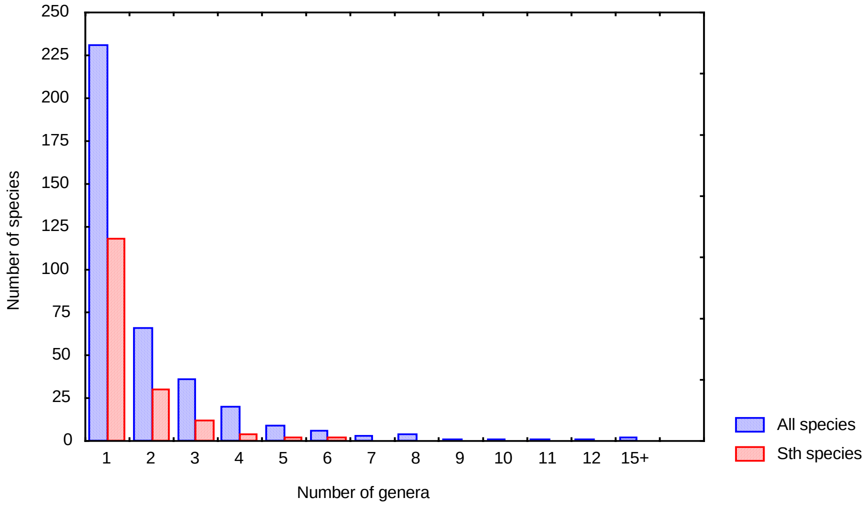


Figure 3.16 Histogram showing generic diversity of southern Australian echinoderms and decapods. Southern species are those that are restricted to south of latitude 30°S.

3.4 Discussion

3.4.1 Pattern analyses

The ordination diagrams presented emphasise both strong longitudinal and latitudinal gradients. There is considerable turnover of species from west to east with peaks near the endpoint of each subregion. Species richness is broadly similar across the coastline with peaks along the east and west coasts and in areas of faunal overlap near the subregional end points. A low-point of species richness occurs in southern Tasmania. Five primary subregions are identifiable from the cluster diagrams:

- the subtropical west coast extending south to Perth;
- the south-west coast from Perth to the South Australian Gulfs;
- the South Australian Gulfs to central Victoria and Tasmania;
- Wilsons Promontory to Sydney; and
- the subtropical region north of Sydney.

Longitudinal variation includes a significant turnover of species but little change in species richness while latitudinal variation includes both species turnover and a decline in species richness with higher latitudes. This longitudinal turnover of species is evident in Victoria where there is a 49% turnover of species across the State. The region of most rapid turnover is between Port Phillip Bay and Wilsons Promontory. This pattern was also observed by King (1972) for macro-algae and invertebrates of rocky shores. However, the strong longitudinal turnover of species has not been emphasised in recent community analyses of Victorian intertidal rocky shores (Victorian Institute of Marine Sciences *et al* 1994), estuaries (Moverley and Hirst 1999) or nearshore soft benthos (Coleman *et al* 2000). Possibly the species that turnover within Victoria are rare in occurrence, or spatially aggregated, and do not contribute significantly to the multivariate analyses used in these studies

3.4.2 Effects of sea surface temperature on species richness

There have been numerous explanations for the latitudinal gradient in species richness. Roy *et al* (1998) tested four explanations against gastropod distributions along the east and west coasts of America. Roy *et al* (1998) could not explain the pattern by the available size of the continental shelf at each latitude (species-area effect), latitudinal differences in the length of species ranges or recent faunal histories (species extinction rates). However, the observed pattern was significantly correlated with sea surface temperature.

The results of this study indicate similar findings by Roy *et al* (1998): there was neither a relationship between species richness and the available area of continental shelf nor a correlation between species richness and average range size. However the observed pattern in species richness was significantly correlated with sea surface temperature and latitude. As expected, however, further analysis found sea surface temperature and latitude to be highly autocorrelated.

3.4.3 Other factors influencing patterns of marine biogeography

The distribution of species in southern Australia is not strictly temperature controlled. Northern distributional limits in particular show little symmetry across southern Australia with most species tolerating higher temperatures on the east coast.

Species with a detectable southern temperature limit fall into two groups:

- a group of tropical species that range further along the west coast than east coast; and
- a group of species that do have a similar temperature limit on both coasts.

There are many possible reasons for lack of symmetry between eastern and western temperature limits including:

- biological interactions (eg competition, predation, availability of food resources);
- environmental variability (eg availability of habitat, seasonal currents); and
- the possible disequilibrium of species ranges following the last glaciation.

Mass spawning at the period of peak flow of the Leeuwin current has been used to explain the presence of corals at southern latitudes in south-western Australia (Wilson and Allen 1987), and may account for the increased penetration of tropical species on the west coast reported herein.

Historical patterns of range shifts require further study. One well-documented example, the arcoid bivalve *Anadara trapezia*, illustrates the complex interaction between range, available habitat and temperature (Kendrick *et al.* 1991). *Anadara trapezia* is currently restricted to estuaries in eastern Australia from Port Phillip Bay in Victoria to central Queensland (19°S) and is also found in one small population at Albany in Western Australia. It tolerates a wide range of temperatures and has a high dispersal capability and yet does not occur today in the South Australian Gulfs or in estuaries on the west coast. Nevertheless it was ubiquitous across southern Australia during the last two interglacials (isotope stages 5e and 7) even reaching New Zealand. It was common 6,500 year ago in the Tamar estuary in northern Tasmania but is absent today (Goede *et al* 1995).

Published data are too fragmentary to permit the detailed analysis of local faunal histories within southern Australia. Well-documented molluscan faunas from the Roe Calcarenite in Western Australia (Ludbrook 1978) and the Point Ellen Formation in South Australia

(Ludbrook 1983) now considered to be late-Pliocene (Kendrick *et al* 1991) contain 65 - 70% extant species. The Early Pleistocene Jandakot bed near Perth is estimated to have 10 - 15% extinct molluscan species (Darragh and Kendrick 1971). Middle and late Pleistocene molluscan faunas (isotope stages 2 - 7) are composed entirely of recent species with a few species exhibiting range shifts to the south during warmer interglacials (Jennings 1959; Valentine 1965; Colhoun *et al* 1982; Ludbrook 1984; Gill 1988; Kendrick *et al* 1991). This is consistent with marine fossil faunas from North and Central America that show pulse extinction and speciation events during the Pliocene, approximately 2 million years ago, at the beginning of the glacial-interglacial cycles (Jackson 1995). Subsequent glacial cycles have induced shifts in the range of species with changing water temperatures but relatively few extinctions (Jackson 1995).

Nevertheless such range shifts could result in extinctions if stenothermal species at the limits of their range are pushed off the ends of land masses. For example, South Africa has lost most of its Gondwanan marine fauna (Edgar 1986). Without replenishment, this process would create a latitudinal gradient of diversity. This process may have occurred in the cool-temperate fauna of south-eastern Australia, producing the lower levels of species richness observable in Tasmania today. Currently 9% of the echinoderms and decapods occurring in southern Australia are restricted to the relatively cool-waters of south-eastern South Australia, western and central Victoria, and Tasmania. The south-eastern Australian fauna can be directly traced back to the early Tertiary (Darragh 1985). It is of cool-temperate Gondwanan origin, dating from the period when the coast of eastern Australia was contiguous with what is now Antarctica and Chile (Poore 1994). Dispersal of additional cool-water species to Australia on Southern Ocean currents has become less likely over time as the Australian continental plate has drifted northward.

Species richness is a product of speciation as well as extinction. There is little evidence for extensive evolutionary radiation amongst southern Australian echinoderms or decapods. There are relatively few speciose genera. Most of these are widespread in other regions and probably only one is endemic to southern Australia. There are a number of endemic genera with 1 - 3 species but these endemics must be treated with caution as the current pattern of endemism may have resulted from extinctions in other regions. The ophiuroid genus *Ophiocrossota*, long known from a single species in Southern Australia, has been recently found in Tertiary beds of North America (Blake and Allison 1970; Blake 1975). Rowe and Vail (1982) have estimated that 70% of Tasmanian echinoderms are of Indo-Pacific origin. This relationship implies that speciation has occurred at the range margins of tropical species as well as evolving from an endemic fauna.

In summary, a hypothesis to explain the pattern of marine biogeography and species richness in southern Australia is:

- the continual invasion and speciation of tropical species as Australia has split from Gondwana and drifted northward;
- progressive extinction of some Gondwanan cool-temperate species at the limits of their range;
- a low level of immigration of additional cool-temperate species; and
- some in-situ endemic speciation.

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